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Infant color vision: sharp chromatic edges are not required for chromatic discrimination in 4-month-olds

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Abstract

In our previous demonstrations of chromatic discrimination in infants, we have used test and surround fields of different chromaticities that abutted each other at sharp chromatic edges. In order to see whether sharp chromatic edges are necessary for infants to make chromatic discriminations, 16-week-old infants were tested with three stimulus configurations in which sharp chromatic edges were eliminated. The three edge manipulations involved black borders, a dark surround, or blurred edges around the chromatic test field. In each case red, green, and violet test fields were used. Although performance decreased when sharp chromatic edges were eliminated, observers' percent correct scores remained clearly above chance for eight of the nine discriminations (three colors \times three edge manipulations). We argue that all three edge manipulations reduce the likelihood of mediation of chromatic discrimination by M (magnocellular) cells. These data thus provide evidence that young infants have functional P (parvocellular) pathways, and use them for making chromatic discriminations. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Since the mid 1970s, data from several laboratories have established that infants 2 months of age and older can make chromatic discriminations. In the paradigm used in our laboratory, infants have been presented with a test stimulus of one color — say, red — embedded in a white or yellow surround, and tested with a forced-choice preferential looking (FPL) paradigm (Teller, 1979). Test and surround fields have been sharply juxtaposed at a chromatic edge. Under these conditions, most 2- and 3-month-olds make chromatic discriminations when chromatic differences are large (Peeples & Teller, 1975; Teller, Peeples & Sekel, 1978; Hamer, Alexander & Teller, 1982; Packer, Hartmann & Teller, 1984; Varner, Cook, Schneck, McDonald & Teller, 1985; Clavadetscher, Brown, Ankrum & Teller, 1988).

But what mediates these chromatic discriminations? There are two major options. First, infants may have color vision in the ordinary sense that they preserve information about the wavelength compositions of the test stimulus and the surround. But alternatively, infants could be using edge cues as the basis of their responses. That is, the test stimulus and the juxtaposed surround make a sharp chromatic edge. As the infant's eyes move, the edge moves across the retina. Infants' visual systems might register the motion of the chromatic edge (cf. Schiller & Colby, 1983; Lee, Martin & Valberg, 1989; Dobkins & Albright, 1993), while not preserving information about the wavelength compositions of the two fields per se.

In other paradigms that have been used to study infant color vision, stimuli that are separated in space and/or time are used. These studies are therefore less vulnerable to the possibility of mediation by edge cues. For example, Bornstein (1975) tested infants' color preferences with single chromatic stimuli or spatially separated pairs of chromatic stimuli presented against a dark surround. Four-month-olds demonstrated clear

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chromatic preferences, implying chromatic discrimination. Similarly, Oster (1975) tested infants with complex displays consisting of either nine grey squares of different luminances, or eight grey squares and one chromatic square. She showed that 2.5-month-old infants prefer the stimulus that includes the chromatic square. Habituation studies, which involve separation of the habituation stimulus from the test stimulus in time, also reveal dishabituation to a stimulus of a novel color in both 4-month-olds (Bornstein, 1976) and newborns (Adams & Courage, 1998). Finally, Schaller (1975) used conditioned operant fixation, and showed that 11–12-week-old infants can learn to fixate either a red or a green checkerboard.

These studies collectively make it unlikely that infants rely solely on edge cues to make chromatic discriminations. Nonetheless, we wished to find out whether edge cues play a major role in infant color vision, particularly in the case of the juxtaposed stimulus fields traditionally used in our laboratory. Thus, the purpose of the present set of experiments was to eliminate the sharp chromatic edge between the test and surround fields. We manipulated this edge in three different ways, to see whether infants can still make chromatic discriminations.

2. Methods

2.1. Overview

Following the FPL paradigm previously used in our laboratory, a test field was embedded to either the left or the right of center of a video display. Three experiments were performed, with the border around the test stimulus being varied in a different way in each experiment. In the *black borders* condition (expt. 1), $8 \times 8^\circ$ square test fields were used, embedded in a yellow surround. 0.5° wide black borders surrounded both the test field and a corresponding yellow standard field (a piece of the yellow surround) on the opposite side of the monitor. In the *dark surround* condition (expt. 2), we continued to use $8 \times 8^\circ$ square fields. The video monitor was set to its black value, except for a test square on one side of the screen and a yellow standard square on the other. Both of these conditions eliminate the sharp chromatic edge by replacing it with high contrast luminance-based edges. Moreover these edges are equated on both sides of the display.

In the *blurred edge* condition (expt. 3), the stimulus was a circular Gaussian blob with a half-height, full-width of 10° , presented on only one side of the screen, with a yellow surround. This condition eliminates the

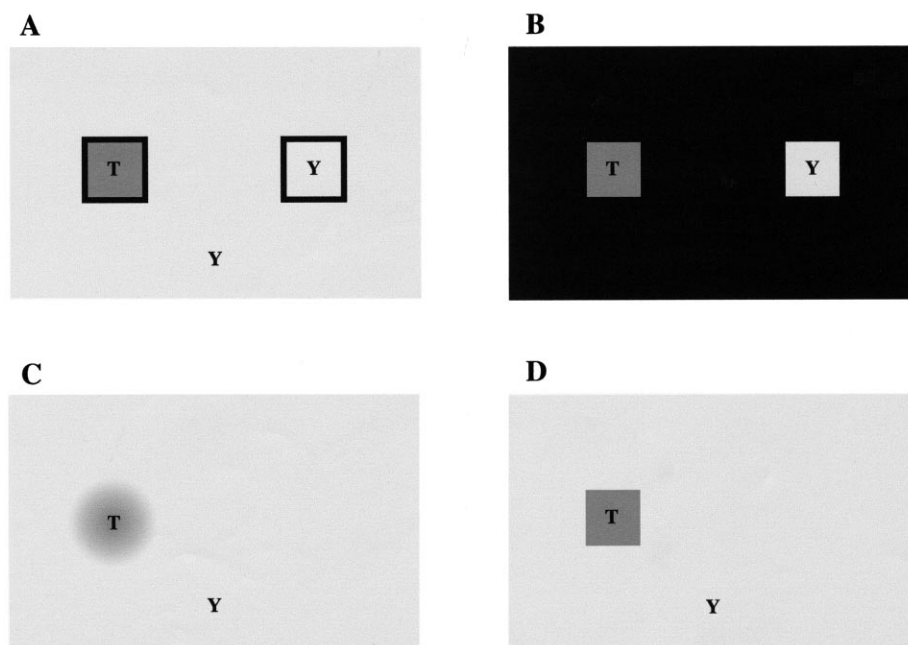


Fig. 1. The stimulus configurations. (A) Black borders (expt. 1). $1/2^\circ$ black borders surrounded the $8^\circ \times 8^\circ$ square test stimulus and a corresponding region of the yellow surround on the opposite side of the display. (B) Dark surround (expt. 2). The display was dark except for an $8^\circ \times 8^\circ$ square test stimulus on one side and a corresponding yellow standard stimulus on the other side. (C) Blurred edges (expt. 3). The stimulus was a circular Gaussian blob with a half height, full width of 10° , embedded in the yellow surround. (D) Control conditions. Sharp-edged control stimuli were also tested in each experiment. The control stimulus was a sharp edged $8^\circ \times 8^\circ$ square (shown) or 10° circle (not shown), depending on the shape of the stimulus in the corresponding manipulated edge condition. T, test stimulus; Y, yellow surround or standard stimulus.

sharp chromatic edge by blurring it dramatically. All spatial frequencies above about 0.2 c/deg were greatly attenuated in this condition.

Each of the three experiments (Fig. 1) also included a control condition — sharp bordered stimuli embedded in the yellow surround — as previously used in chromatic discrimination experiments from our laboratory. Stimuli in each control condition were of the same size and shape as the stimuli in the corresponding test condition. The control conditions were very much the same for all three experiments, and their results were all highly similar (see Results, below).

2.2. Subjects

Infant subjects were 16-week-olds recruited from the Infant Studies Subject Pool at the University of Washington. Parents were paid for their infants' participation and informed consent was obtained. All infants were born within ± 14 days of their due date. Male infants with relevant family histories of color vision deficiency were excluded from the study. Infants were tested for four to five sessions within a 1-week time span beginning on the 110th postnatal day ± 3 days.

Thirty-one infants provided usable data for the three experiments (11 for expt. 1; 10 for expt. 2; 10 for expt. 3). Data sets were discarded when the infant either completed fewer than 20 trials per data point (five infants) or performed below 85% on the 'easy' trials (black/yellow checkerboards interspersed randomly into the stimulus sequence) (three infants). The overall testability rate was therefore 79%.

2.3. Apparatus and stimuli

2.3.1. Apparatus

Stimuli were presented on a color video system consisting of a Mac IICI controlling a calibrated Barco COCT 6451 monitor. The monitor subtended $53 \times 40^\circ$ at the test distance of 38 cm.

2.3.2. Test stimuli

The monitor surround for experiments 1 and 3, and the standard stimulus in experiments 1 and 2, were yellow with CIE chromaticity coordinates of (0.49, 0.43) and a luminance of 14 cd/m². Test stimuli were either 8° disks or 10° squares, displayed in the centers of the right and left sides of the monitor. Three chromatic test stimuli were used, with CIE coordinates of (0.61, 0.33), (0.29, 0.61) and (0.31, 0.17). All chromatic test stimuli were set to the maximum available instrument contrast. Although the color appearance of these stimuli for infants is obviously unknown, for convenience they will be called *red*, *green* and *violet*, respectively. The red and green stimuli were designed to probe the r/g (L – M) channel of color vision while

holding the S-cone signal constant, while the violet stimulus was designed to probe the tritan (S – (L + M)) channel while holding the L- and M-cone signals constant (Boynton, 1979; Derrington, Krauskopf & Lennie, 1984). Video-generated stimuli that isolate the (L – M) and (S – (L + M)) channels in adults also provide adequate isolation of these channels in infant subjects (Suttle and Banks, 1999; and see below concerning luminance controls).

In addition to the red, green and violet test stimuli, both *black* and *bright yellow* test stimuli were used. The black stimulus was set to nominal zero luminance and the bright yellow stimulus was set to twice the base luminance (28 cd/m²). The black stimulus was not used in the dark surround condition (expt. 2). The purpose of these stimuli was to get an indication of the infant's sensitivity to luminance differences under the present conditions, and (if possible) to use these data to argue against the possibility that any inadvertent luminance mismatches between the test fields and the surround might mediate the results obtained with chromatic stimuli.

2.3.3. Isoluminance settings

The luminances of the chromatic test stimuli were matched to the 14 cd/m² yellow surround according to Judd's modified V_λ . Prior research has shown that adult photometric matches provide a close approximation to infant photometric matches (Teller & Lindsey, 1989; Bieber, Volbrecht & Werner, 1995; Brown, Lindsey, McSweeney & Walters, 1995). Moreover, infants' sensitivity to luminance differences is poor; in consequence, small luminance mismatches cannot mediate discrimination in infant subjects. This issue has been discussed in detail by Brown et al. (1995) and Dobkins and Teller (1996).

2.3.4. Cone and rod contrasts

For incremental and decremental stimuli such as those used here, it is customary to define contrast as $\Delta I/I$ (the *difference* in intensity between the test field and the surround field, divided by the intensity of the surround field). By this definition, test fields that provide either an increment to twice the intensity of the surround or a decrement to zero intensity provide a contrast of 100%, and contrast increments much larger than 100% can be produced. When our stimuli have contrasts greater than 100%, we also state the multiplicative increase in intensity produced by the stimulus; e.g. a contrast of 1500% is a 16-fold increase.

Each of the test stimuli produced a spatial contrast in the matrix of cones of each type: $\Delta L/L$ for the L-cones; $\Delta M/M$ for the M-cones; and $\Delta S/S$ for the S-cones. The red and green stimuli embedded in the yellow surround produced contrasts of 15, 37 and 0% in the L-, M- and S-cones, respectively; the violet stimuli produced con-

trasts of 0, 0 and 1500% (a 16-fold increase), respectively; and the black and bright yellow stimuli produced contrasts of 100% for all receptor types.

All stimuli in the yellow-surround conditions also produced significant contrast ($\Delta R/R$) for the rods. The rod contrasts were 61, 61, and 161% (a 2.6-fold increase) for the red, green and violet stimuli, respectively. In order to sort out whether rods, cones or both mediate the discriminations for each stimulus, estimates of thresholds for each individual receptor type under our conditions, and a theory of how their signals combine to yield the overall behavioral threshold, would be required. In the absence of such knowledge, mediation of the infants' responses by rod-initiated signals cannot be ruled out. However, we note that rod mediation seems particularly unlikely in the case of the violet stimulus embedded in the yellow surround, since the S-cone contrast (1500%) is so much larger than the rod contrast (161%) for this wavelength combination.

2.4. Procedures

Forced-choice preferential looking, or FPL (Teller, 1979) was used in all three experiments. Infants were held by the observer in a vertical position in front of the stimulus display. Using an auxiliary video system, the observer watched the infant's face and eye movements, and made a forced-choice judgment of the location of the test stimulus on each trial. Trial-by-trial feedback was provided.

Infants were tested for as many trials as possible in four to five test sessions within a 1-week time span. In the retained data sets, the overall number of trials per test stimulus ranged from 20 to 63, with a mean of 41. In each experiment, all test stimuli and both experimental and control conditions were run on the same infant in a within-subjects design.

2.5. Data analysis

Percent correct scores were averaged across infants within each condition. The error bars on all figures represent the standard errors of the percent correct scores. Points without visible error bars had standard errors less than 1 percentage point. Significance levels are stated in the text only in cases in which the outcome is not obvious by visual inspection. Due to the large numbers of infants and the large numbers of trials used, percent correct scores below 55% are sometimes statistically reliably above chance (50%), but we do not consider these differences to be meaningful.

In our previous work on infant color vision, we have used a rather stringent definition of color vision: each infant was tested with several different luminances of the chromatic test field, and was said to make a chromatic discrimination only if he or she performed at or

above 75% correct in an FPL task at *every* luminance level. In the present study, we depart from our previous strict design and scoring criterion. Infants were tested only at isoluminance as defined by V_λ , and a discrimination was counted as successful if a group of infants performed reliably and meaningfully better than chance, even if this performance fell below 75% correct.

2.6. Eight-week-olds

Eight-week-old infants were also tested in the blurred-edge condition, but their performance, while above chance for the red and violet test stimuli, was too marginal to allow any strong conclusions. Informal observations also suggested that 8-week-olds do not perform well in the black border and dark surround conditions.

Unfortunately, the present set of experiments is asymmetrical in power, in the sense that positive results are more theoretically interpretable than negative results. In the black border and dark surround conditions, the extraneous edges on both sides of the display turn the experiment into a preference experiment (cf. Bornstein, 1975) as opposed to a detection experiment; and in the blurred edge condition elimination of spatial frequencies above 0.2 cy/deg should in itself make these stimuli less visible (Banks & Salapatek, 1976). Thus, an infant's failure to make a chromatic discrimination has alternative explanations, and need not indicate the necessity of sharp chromatic edges per se. Other paradigms will need to be developed to pursue this question at younger ages.

3. Results

The data from all three experiments are plotted in Fig. 2. The control conditions (sharp-edged stimuli) are shown in panels A and B, with the black and bright yellow stimuli shown in panel A and the chromatic stimuli shown in panel B. Recall that all three control conditions were identical, except that the stimuli were 8° squares in experiments 1 and 2 and 10° circles in experiment 3. Nearly all scores in the control conditions are above 75% correct, with the mean for the chromatic conditions being 80.8%. These data thus confirm and extend earlier reports (cited in Section 1) that infants in the 3–4-month age range can make chromatic discriminations.

The three manipulated edge conditions are shown in panels C and D, with the black and bright yellow stimuli shown in panel C and the chromatic stimuli in panel D. Panel C shows that when sharp edges are eliminated, 16-week-old infants are much more successful at discriminating the black stimuli than the bright yellow stimuli from the surround. The mean value for

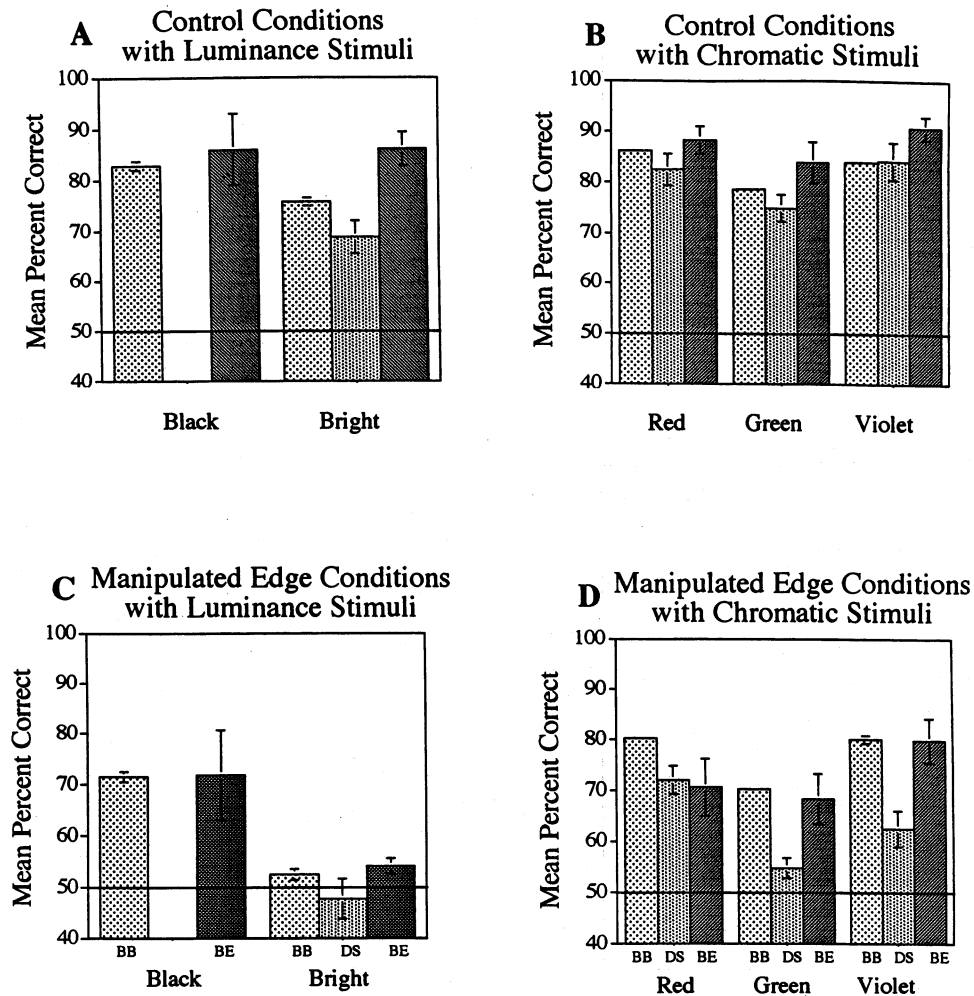


Fig. 2. Results of experiments 1–3. Control (sharp-edged) conditions (panels A,B) versus manipulated edge conditions (panels C, D); Luminance-modulated stimuli (panels A, C) versus chromatic stimuli (panels B, D). The black stimulus was not used in the dark surround condition. For the manipulated edge conditions (panels C, D), the labels along the abscissa provide mnemonics for the three experiments: BB, black borders (expt. 1); DS, dark surround (expt. 2); BE, blurred edge (expt. 3). Stipple patterns in panels A and B versus C and D identify the experiment in which each set of control data was generated. The ordinate shows the observer's mean percent correct. The solid horizontal line in each figure denotes chance performance. The error bars show ± 1 SEM. Error bars are omitted for standard errors ≤ 1 percentage point. In all cases, manipulating the edge decreases performance, especially for the bright yellow stimuli; but performance remains reliably above chance for the three chromatic stimuli (red, green and violet) in eight out of nine cases. Performance is marginal for the green stimulus in the dark surround condition.

the black stimuli was 71%, whereas for the bright yellow stimuli the mean value was essentially at chance at 52%.

For chromatic stimuli (panel D), each of the performance scores in the manipulated edge conditions was reduced from the corresponding control condition (panel B). Nonetheless, the mean percent correct across all three experiments was 74% for red; 64% for green, and 74% for violet. All but one of nine conditions remained reliably and meaningfully above chance. The exception is the green test stimulus in the dark surround experiment (expt. 2), for which performance was marginal (55% correct; cf. Bornstein, 1975).

4. Discussion

The fundamental empirical question posed by the present set of experiments was: can 16-week-old infants make chromatic discriminations in the absence of sharp chromatically defined edges? The answer to this question is yes. Whether sharp chromatic edges are replaced with luminance edges on both sides of the display, or by blur that eliminates all but the lowest spatial frequencies, infants continue to make chromatic discriminations.

Combining across all three manipulated edge conditions, scores were reliably and meaningfully above

chance for eight out of the nine chromatic stimuli under the critical test conditions, and marginally but statistically reliably above chance for the ninth condition. Moreover, the same infants performed near chance with 100% luminance increments under the same edge conditions. Thus, it is unlikely that the infants' performance with chromatic stimuli was supported by residual luminance mismatches. We conclude that 16-week-old infants can make chromatic discriminations — respond differentially to lights of different wavelength composition — in the absence of sharp chromatically defined edges.

We now turn to the theoretical interpretation of this finding. In early visual processing, adult chromatic discrimination is classically ascribed to the P, or parvocellular pathway (and more recently the K, or koniocellular pathway; Dacey & Lee, 1994; Hendry and Calkins, 1998) rather than to the M, or magnocellular pathway. But there is accumulating evidence that infants' detection thresholds for red/green gratings display many of the psychophysical signatures classically seen for luminance-modulated rather than chromatic stimuli. These signatures include motion:detection (M:D) ratios near one (Dobkins and Teller, 1996), and chromatic temporal contrast sensitivity functions (tCSFs) that are bandpass rather than lowpass, and fall off only at temporal frequencies above about 10 Hz (Dobkins, Lia & Teller, 1997; Dobkins, Anderson & Lia, 1999).

The hypothesis that infants might use signals carried in their M pathway rather than their P pathway for mediating the detection of chromatic gratings can be called the *M-cell dominance hypothesis*. Moreover, it is useful to distinguish between strong and weak versions of this hypothesis. The strong version would suggest that P cells are not functional in infants, and that all visual functions must be mediated by M-cells. The weak version would suggest that P-cells are functional, but are differentially reduced in contrast sensitivity with respect to M-cells. As an example of the latter, Dobkins et al. (1999) have modelled the red/green chromatic tCSFs of 3-month-olds by assuming that the contrast thresholds of P-cells are reduced about 0.4 log unit more than those of M-cells, with the result that M-cells mediate the chromatic tCSF at all but the lowest temporal frequencies.

If M-cells do mediate detection of chromatic differences in infants, they might do so in either of two ways. The major possibility is that they do so with edge transients. Schiller and Colby (1983), Lee et al. (1989) and Dobkins and Albright (1993) have shown that M-cells produce a transient response to an isoluminant red/green chromatic edge moving across their receptive fields. When grating stimuli are used, these transient responses take the form of frequency-doubled modulation of the M-cell response. In our standard stimulus

display, eye movements move the chromatic border between test and surround fields across the receptive fields of M-cells. The resulting M-cell transients produce visual signals at the edges of the test field; and the infant might stare in the direction of the test field and its edges without any actual preservation of wavelength information per se.

A recent experiment by Lia, Dobkins, Palmer and Teller (1999) argues against mediation of infant chromatic discriminations solely by frequency-doubled signals. In addition to their capacity to make chromatic discriminations with static stimuli, infants can also respond to moving red/green isoluminant gratings with directionally-appropriate eye movements (Teller & Lindsey, 1993; Brown et al., 1995; Teller and Palmer, 1996). Lia et al. (1999) tested 3-month-olds with sinusoidal gratings shifting in quadrature. A grating in quadrature motion undergoes a 90° phase shift each time it moves. Thus, the edge in frame $N + 1$ is halfway between two edges in frame N , and edge locations cannot serve as correspondence cues for determining the direction of motion. Lia et al. (1999) found that infants still produce directionally-appropriate eye movements in response to quadrature shifted red/green isoluminant gratings.

The present experiments with stationary stimuli, along with that of Lia et al. (1999) with moving stimuli, argue against mediation of infant chromatic discriminations solely by M-cell transients. The fact that infants discriminate the violet test field from the yellow surround in the present experiment argues particularly against the M-cell transients hypothesis, since M-cells do not show transients in response to moving tritan stimuli (Lee et al., 1989).

The second way that M-cells could mediate infant chromatic discrimination is via *non*-frequency-doubled signals. This possibility arises from the fact that the red/green isoluminance points of M-cells vary across the population of M-cells (Derrington et al., 1984; Dacey and Lee, 1994). Thus there is no luminance ratio in the chromatic stimulus that nulls the responses of all M-cells at the same time; and the remaining M-cell signals could mediate the detection of chromatic differences (Dobkins and Albright, 1998; Lia et al., 1999). However, the very large luminance contrasts in the present black borders and dark surround conditions should saturate the responses of M-cells, thus blocking their use in signalling chromatic differences; yet infants continue to respond to chromatic differences.

In summary, 16-week-old infants can respond to chromatic differences between stimuli that are spatially separated by black borders, or embedded in black surrounds, to equate and saturate edge cues on both sides of the visual display. They can also respond to chromatic stimulus fields blurred to remove all but very low spatial frequencies, and thus greatly attenuate or

eliminate edge cues. Thus the present data militate against the strong form of the M-cell dominance hypothesis — that there are no functional P-cells, and that M-cells mediate all visual functions in infants, including chromatic discriminations. It seems increasingly likely that young infants have functional P-cell systems and can use them for making chromatic discriminations, at least under the conditions tested here.

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